

Report

Spontaneous Motor Entrainment to Music in Multiple Vocal Mimicking Species

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Summary

The human capacity for music consists of certain core phenomena, including the tendency to entrain, or align movement, to an external auditory pulse [1–3]. This ability, fundamental both for music production and for coordinated dance, has been repeatedly highlighted as uniquely human [4–11]. However, it has recently been hypothesized that entrainment evolved as a by-product of vocal mimicry, generating the strong prediction that only vocal mimicking animals may be able to entrain [12, 13]. Here we provide comparative data demonstrating the existence of two proficient vocal mimicking nonhuman animals (parrots) that entrain to music, spontaneously producing synchronized movements resembling human dance. We also provide an extensive comparative data set from a global video database systematically analyzed for evidence of entrainment in hundreds of species both capable and incapable of vocal mimicry. Despite the higher representation of vocal nonmimics in the database and comparable exposure of mimics and nonmimics to humans and music, only vocal mimics showed evidence of entrainment. We conclude that entrainment is not unique to humans and that the distribution of entrainment across species supports the hypothesis that entrainment evolved as a by-product of selection for vocal mimicry.

Results

Auditory-motor entrainment, the ability to align motor actions with an external auditory beat, has been commonly assumed to be a uniquely human capacity [4–11]. However, it has recently been proposed that auditory-motor entrainment (henceforth “entrainment”) emerged as a by-product of selection for vocal mimicry, leading to the prediction that only vocal mimicking animals will be able to entrain [12, 13]. By this

hypothesis, vocal mimicry would be a necessary, although likely not sufficient, condition for entrainment.

Vocal mimics form a relatively small group, including humans, three avian clades (songbirds, parrots, and hummingbirds [14]), two marine mammal clades (cetaceans [15, 16] and pinnipeds [17]), elephants [18], and some bats [19] (see the [Supplemental Data](#) available online). If vocal mimicry were a necessary precondition for entrainment, we would expect to find the capacity for entrainment only in vocal mimicking species. This view predicts that other factors (e.g., phylogenetic proximity to humans, exposure to music, movement imitation, and/or complex social structure) cannot enable entrainment in the absence of vocal mimicry.

Here we report evidence of entrainment from detailed case studies of two avian subjects, both proficient vocal mimics (parrots). In addition, we test the claim that vocal mimicry is necessary for entrainment by performing a broader comparative exploration of entrainment in hundreds of species.

Case Studies

Subject 1, a well-studied African grey parrot [20] (*Psittacus erithacus*), was video-recorded while exposed to novel naturalistic rhythmic musical stimuli at two tempi (120 and 150 beats per minute [bpm]) in the absence of visual rhythmic movement. Subject 2, a sulphur-crested cockatoo [21] (*Cacatua galerita eleanora*), was recorded while exposed to novel natural rhythmic music and one familiar piece of music with tempi ranging from 108 to 132 bpm (see [Supplemental Experimental Procedures](#)) in the absence of continuous human movement. Neither subject had been explicitly trained to produce movement in response to acoustic material.

During presentation of the stimuli, both subjects spontaneously displayed periodic (regularly spaced) movement in the form of head bobbing; subject 2 also displayed periodic foot lifting (see [Movies S1 and S2](#)). We assessed whether the subjects' periodic movements were entrained to the musical beats by analyzing the frequency and phase of the subjects' movements. We collected data on intentional human entrainment to the same stimuli by asking human subjects to tap a button to the beat of the same musical stimuli used with avian subjects. These human data served both as a measure of the location of the musical beats as well as a measure of the range of error acceptably present in entrained movement. We then examined the extent to which the avian movements aligned with the intentionally entrained tapping of the human subjects (see [Figure 1](#) and [Supplemental Experimental Procedures](#)).

Multiple analyses comparing avian movement to the musical beat allowed for convergent evidence of entrainment. First, we asked whether subjects' movements maintained a more consistent phase relationship with the musical beat than expected by chance, using the Rayleigh test with unspecified mean direction [21–23]. Because the motor and cognitive systems introduce noise to periodic movement, maintaining a consistent phase with the external stimulus is extremely unlikely without real-time error correction to actively realign with the beat (i.e., entrainment) [1]. Thus, consistency of phase over many beats is strong evidence of entrainment. Second,

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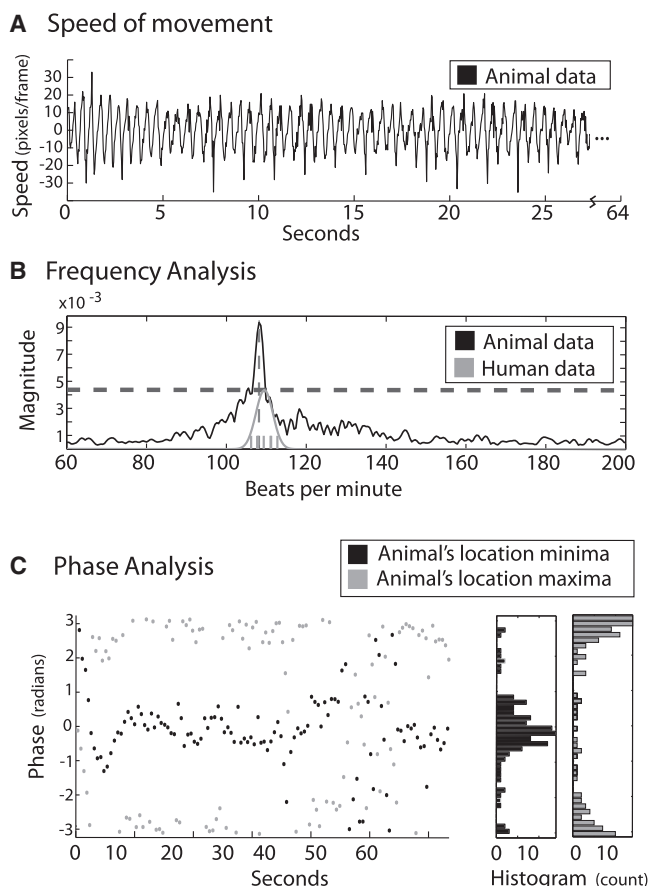


Figure 1. Visualizations of Methods

(A and B) We videotaped nonhuman subjects while they moved in response to music and then coded the location of each subject's head in each frame. To compute the magnitude of motion at each frequency, we took the derivative to obtain the speed of movement (A) and performed a Fourier transform to convert this signal to frequency space (black waveform in [B]). To test whether subjects were moving at a consistent frequency, we used a Monte Carlo simulation to estimate the magnitude (at any frequency) that would be obtained less than 5% of the time by random head bobbing ($p < 0.05$; dashed line in [B]), which served as the threshold for significance. We then asked whether the animals were moving at the correct frequency by comparing the peak (modal) frequency from the animal data to the range of modal frequencies of human tapping for the same set of stimuli, to see whether the peak frequency in the animals' movement fell within 2 SD of the mean of the distribution of human subjects' modal tap frequencies (maximum-likelihood Gaussian; light gray waveform in [B]). (C) We asked whether the movements were in consistent phase with the musical beat as perceived by a human subject or an automated beat tracker [34] (see Supplemental Experimental Procedures), using the Rayleigh test with unspecified mean direction [22]. We then additionally asked whether the movements were phase matched with the musical beat, using the Rayleigh test with a specified mean direction of zero [22] (see Results). Shown: subject 2, trial 1, head movement.

we asked whether the birds' movements were phase matched (synchronized) with the musical beats. Although this is not a necessary condition for entrainment, human subjects typically phase match when tapping to the beat [1]; thus, avian phase matching would demonstrate an additional way in which the phenomenology of avian entrainment resembles that of human entrainment. To detect phase matching, we used a modified version of the Rayleigh test [22], this time specifying a mean direction of zero (identical phase).

To provide convergent evidence for entrainment, we ran two additional tests to determine (1) whether the periodicity of movement was likely to have been due to chance and (2) whether the modal frequency of movement matched the modal frequency of the musical beats as perceived by human subjects. We performed a Fourier transform on the avian subjects' speed-of-movement function to identify the extent to which the subject was moving at each frequency. If the subject was moving periodically (i.e., with consistent frequency), we saw a peak at the frequency range most present in the movement. We used a Monte Carlo simulation to determine whether the periodicity was extensive enough to have been unlikely by chance ($p < 0.05$) (Figure 1). We then determined whether the animal's frequency matched the musical beat by asking whether the modal frequency of the animal's movement (the peak of the Fourier transform) fell within the range of modal frequencies of human subjects' tapping to the same set of auditory stimuli.

Case 1: Subject 1, African Grey Parrot

For four of the six presentations of the 120 bpm stimuli, subject 1's head bob movements maintained a significantly consistent phase relationship with the musical beat ($p < 0.05$ via the Rayleigh test with unspecified mean direction; see Table 1). The probability of observing these data due to chance was less than 1 in 10^8 . Subject 1 also showed significantly periodic (consistent-frequency) movement in all six trials ($p < 0.05$ for all six trials; $p < 0.01$ for five of six trials). Subject 1 thus showed strong evidence of entrainment.

Subject 1's movements were also phase matched with humans' taps to the musical beat in one of the four consistent-phase trials ($p < 0.05$ via the Rayleigh test with a specified mean direction of zero), showing an additional parallel between subject 1's behavior and human entrainment.

Subject 1 did not show periodic movement in response to the 150 bpm stimuli. This frequency may have exceeded the range of tempi to which entrainment is possible for this subject. Unfortunately, it was not possible to further explore this subject's behavior because of his unexpected death [24].

Case 2: Subject 2, Sulphur-Crested Cockatoo

Subject 2's head movements maintained a significantly consistent phase relationship with the musical beat in three of four presentations of rhythmic stimuli ($p < 0.05$). The likelihood of maintaining as consistent a phase relationship by chance was less than 1 in 10^{18} . Subject 2 displayed significantly periodic movement in the same three of four trials ($p < 0.01$ for all three trials). Importantly, these three rhythmic stimuli spanned a wide range of tempi, from 108 to 132 bpm. Thus, subject 2 demonstrated the ability to flexibly entrain movements with musical beats of a variety of speeds.

Subject 2's movements were also synchronized, or phase matched, with the musical beat in each of the three consistent-phase sessions ($p < 0.05$).

In addition to head bob movements, subject 2 also displayed foot-lifting movement in response to the music. Subject 2's foot movement also showed evidence of entrainment: it maintained a significantly consistent phase with the musical beat during four of four trials ($p < 0.05$). In three of four trials, foot movements were phase matched with the beat ($p < 0.05$), significantly periodic ($p < 0.01$), and matched in modal frequency with the musical beat (see Table 1). This response suggests considerable motor flexibility in entrainment, similar to the highly flexible motor response of humans during entrainment [1, 13]. Overall, by matching phase, flexibly entraining to multiple tempi, and involving multiple body parts in

Table 1. Subject 1's and Subject 2's Data by Trial

	Session	Tempo (bpm)	Phase		Frequency	
			Consistent Phase Relationship (*p < 0.05; with humans, autotracker)	Phase Matched (*p < 0.05; with humans, autotracker)	Matched Modal Frequency (Z score; *Z score < 2)	Consistent Frequency (*p < 0.05 under Monte Carlo simulation)
Subject 1, head	1	120	6/8 a *	0/8	0.54*	*
	2	120	1/7*	3/7*	-2.51	*
	3	120	0/8	0/8	5.19	*
	4	120	2/8 a *	0/8	-0.05*	*
	5	120	2/7*	0/7	-1.77*	*
	6	120	0/7	0/7	2.55	*
Subject 2, head	1	108	7/7 a *	7/7 a *	-0.75*	*
	2	111	8/8 a *	8/8 a *	0.04*	*
	3	111	0/8	0/8	-4.50	NS
	4	132	8/8 a *	8/8 a *	-0.41*	*
Subject 2, feet	1	108	7/7 a *	6/7*	-0.68*	*
	2	111	8/8 a *	7/8*	-0.09*	NS
	3	111	1/8 a *	0/8	-9.44	NS
	4	132	8/8 a *	8/8 a *	-0.78*	*

Phase analyses: the Rayleigh test with unspecified mean direction [22] was used to determine whether the animals' movements maintained a consistent phase relationship to the musical beat as perceived by any of the human subjects or computed by an automated beat tracker [34]. The Rayleigh test with a specified mean direction of zero [22] was used to determine whether the animal's movements were synchronized, or phase matched, with the musical beat. Ratio values indicate the number of human subjects whose data significantly matched the animals' data ($p < 0.05$) over the total number of human subjects at the correct metrical level. Only human subjects who tapped at the same metrical level as the animal were included for analysis, so as to maintain the validity of the analyses (e.g., if a subject tapped at a lower (faster) metrical level, this would greatly increase the likelihood of finding synchrony/consistency even if it were not present; see Supplemental Data). Matched modal frequency: Z score refers to location of modal frequency within distribution of human subjects' modal frequencies tapping to the same stimuli; <2 SD was considered matched modal frequency. Consistent frequency: p value refers to likelihood under Monte Carlo simulation (see Results and Supplemental Experimental Procedures); significance implies movement at a consistent frequency throughout the trial (NS = not significant). Tempo refers to the mean of subjects' modal tapping frequencies in beats per minute (bpm). "a" indicates that autotracked beat was phase consistent or phase matched with the subject's movement.

entrainment, subject 2 demonstrates a phenomenology strikingly similar to human subjects.

In summary, these case studies show strong evidence of entrainment in nonhuman animals based on multiple convergent analyses. In addition, a simultaneously collected data set provided convergent evidence of entrainment: In a separate experiment with subject 2 by Patel and colleagues in this issue of *Current Biology*, the tempo of a song that reliably evoked movement was changed by small increments (5%, 10%, etc.), and analyses revealed spontaneous adjustments of movement tempo to match tempo manipulations of the music ([21]).

Claims of human uniqueness are defeated by even one well-documented case study demonstrating the existence of the capacity in a nonhuman animal; here we report entrainment in two nonhuman subjects. These data rule out the claim that entrainment is unique to humans and provide initial support for the hypothesis that vocal mimicry is necessary for entrainment.

To provide further support for this hypothesis, we also tested a group of vocal nonmimics, cotton-top tamarin monkeys, for entrainment with the same set of stimuli, procedures, and analyses that successfully demonstrated entrainment in our avian subjects (see Supplemental Experimental Procedures and Supplemental Results). Of the nine tamarins tested (270 min of video), none showed evidence of entrainment.

Though the results thus far are consistent with the vocal mimicry hypothesis, they are limited by the small sample of subjects, species, and materials. To fully test the vocal mimicry hypothesis, we must ask whether entrainment is truly never present in species lacking the capacity for vocal mimicry. It is therefore necessary to test an extremely broad set of comparative data representing many species, many

individuals of each species, and multiple sessions with the same individual. We performed a systematic analysis of a global video database, which provided the scope of data needed to find evidence of entrainment across a wide range of species and subjects.

Video Database Analyses

The global database used, www.youtube.com, is a video-sharing website consisting of tens of millions of user contributions from a wide range of people across the globe. Users commonly post animal behavior on YouTube, and animals that dance are popular (e.g., one video of subject 2 has over 3 million views). Given the widespread ability and motivation of millions of users to post popular videos, we expect that if animals to which humans are regularly exposed are capable of entrainment, even as a result of training, there is a high likelihood that videos of such activity would be present on YouTube.

There are of course many selection biases associated with the kinds of videos that people post on YouTube (e.g., users posting only the best videos). However, we have no reason to assume that any of these biases would be systematic with respect to our question of interest—the relationship between vocal mimicry and entrainment. In addition, vocal nonmimicking species are much more highly represented on YouTube than vocal mimics (by a ratio of approximately 2:1), increasing our chance of detecting entrainment in vocal nonmimics.

We systematically queried the database for a variety of animal terms plus "dancing," covering a wide range of species commonly in contact with humans (e.g., "cat," "dog," "bird"). For each search, we recorded the first 50 results (as sorted by relevance) and categorized them by a variety of dimensions (presence of an animal, periodic movement, rhythmic sound, potentially entrained). These categorizations were verified

Table 2. Analysis of Videos from Global Video Database

Species	Video	Phase		Frequency	
		Consistent Phase Relationship (*p < 0.05; with humans, autotracker)	Phase Matched (*p < 0.05; with humans, autotracker)	Matched Modal Frequency (Z score; *Z score < 2)	Consistent Frequency (*p < 0.05 under Monte Carlo simulation)
Asian elephant	1	3/8*	1/8*	0.39*	NS
	2	1/8*	0/8	-0.42*	NS
	3	3/8*	3/8*	2.29	NS
	4	0/8	0/8	-1.99*	*
African grey parrot	5	0/9	1/9*	0.68*	NS
	6	7/8 a *	0/8	1.81*	*
	7	1/6*	1/6*	4.96	NS
	8	0/8	0/8	1.56*	*
Blue and gold macaw	9	1/7*	0/7	-9.61	*
	10	1/7*	0/7	3.38	*
Blue-crowned conure	11	2/4*	1/4*	-0.43*	NS
Green conure	12	1/9 a *	1/9*	0.18*	NS
Green-winged macaw	13	0/8	5/8*	-6.18	NS
	14	0/10	0/10	-0.84*	NS
	15	1/8*	0/8	-1.77*	*
Hyacinth macaw	16	0/7 a *	0/7	-6.77	*
Indian ringneck parakeet	17	1/6*	0/6	-0.85*	NS
Moluccan cockatoo	18	1/8 a *	1/8*	-16.28	NS
Nanday conure	19	1/10*	0/10	6.28	NS
	20	0/7	0/7	-0.09*	NS
Peachface lovebird	21	0/1	0/1	0.92*	NS
	22	1/10*	0/10	0.72*	*
Quaker parrot	23	0/1	1/1*	2.80	NS
Sulphur-crested cockatoo	24	7/7 a *	1/7*	0.89*	*
	25	1/2 a *	0/2 a *	0.02*	NS
	26	1/9*	1/9*	0.73*	NS
	27	0/9 a *	0/9	-0.38*	NS
	28	0/2	0/2	-1.64*	*
Sun conure	29	2/7*	0/7	4.43	*
Umbrella cockatoo	30	0/6	3/6*	1.39*	NS
	31	0/8	0/8	-0.83*	*
	32	0/8	0/8	1.56*	NS
	33	0/8	0/8	1.16*	NS

Shown here are analyses for all animals that showed any evidence of entrainment, casting the widest possible net by including any individual that passed even one of our two main measures. Note that all animals are from vocal mimicking species. Scientific names (respectively): *Elephas maximus*, *Psittacus erithacus*, *Ara ararauna*, *Aratinga acuticaudata*, *Aratinga holochlora*, *Ara chloroptera*, *Anodorhynchus hyacinthinus*, *Psittacula krameri*, *Cacatua moluccensis*, *Nandayus nenday*, *Agapornis roseicollis*, *Myiopsitta monachus*, *Cacatua galerita eleanora*, *Aratinga solstitialis*, *Cacatua alba*. See caption from Table 1 and methods in main text for explanation. For full data from all analyzed videos, see Table S2. "a" indicates that autotracked beat was phase consistent or phase matched with the subject's movement.

through reliability testing (10% recoded blind; coders agreed on 96.9% of trials; see Supplemental Experimental Procedures).

We analyzed the musical beat and animals' periodic movement via the same methods as in the case studies above for any video that had been categorized as potentially entrained. We then iteratively performed more specific follow-up searches for groups showing evidence of entrainment and also performed theoretically driven searches for nonhuman primate species, additional vocal mimicking species, and groups of species that are closely related but differ in their vocal mimicry status (e.g., oscine and suboscine birds). These searches were designed to tease apart potential contributing factors for entrainment, such as vocal mimicry, phylogenetic proximity to humans, and extent of experience with humans.

We performed 161 searches, resulting in 3879 unique videos. Of these videos, 1019 featured a nonhuman animal. Importantly, the proportion of videos of vocal nonmimics (53%) was comparable to that of vocal mimics (47%). In addition, a large proportion of videos featured both vocal nonmimicking animals and rhythmic sound (44% of the 406 with rhythmic sound).

Only vocal mimicking species showed evidence of entrainment, even when casting the widest possible net by including any individual that passed even one of our two main measures (maintaining consistent phase, matching frequency). Of the vocal mimicking species, a total of 15 species across 33 individual videos showed evidence suggestive of entrainment, including 14 species of parrot and one elephant species (see Table 2, Figure 2, and Table S2). At least one individual of each of the 15 species maintained a significantly consistent phase relationship with the musical beat ($p < 0.05$). Individuals of 9 of the 15 species were both consistent and phase matched with the musical beat ($p < 0.05$). The modal frequency of movement of 10 of the 15 consistent-phase species matched the frequency of the musical beat, providing convergent evidence for entrainment in the same individuals; we found consistency of frequency that was highly unlikely to have occurred by chance in 9 of the 15 species ($p < 0.05$).

Vocal nonmimics showed no evidence of entrainment by any of our measures, despite significant effort by many individuals to train dance-like behavior (e.g., "canine freestyle," in which people spend years training dogs to compete in dance

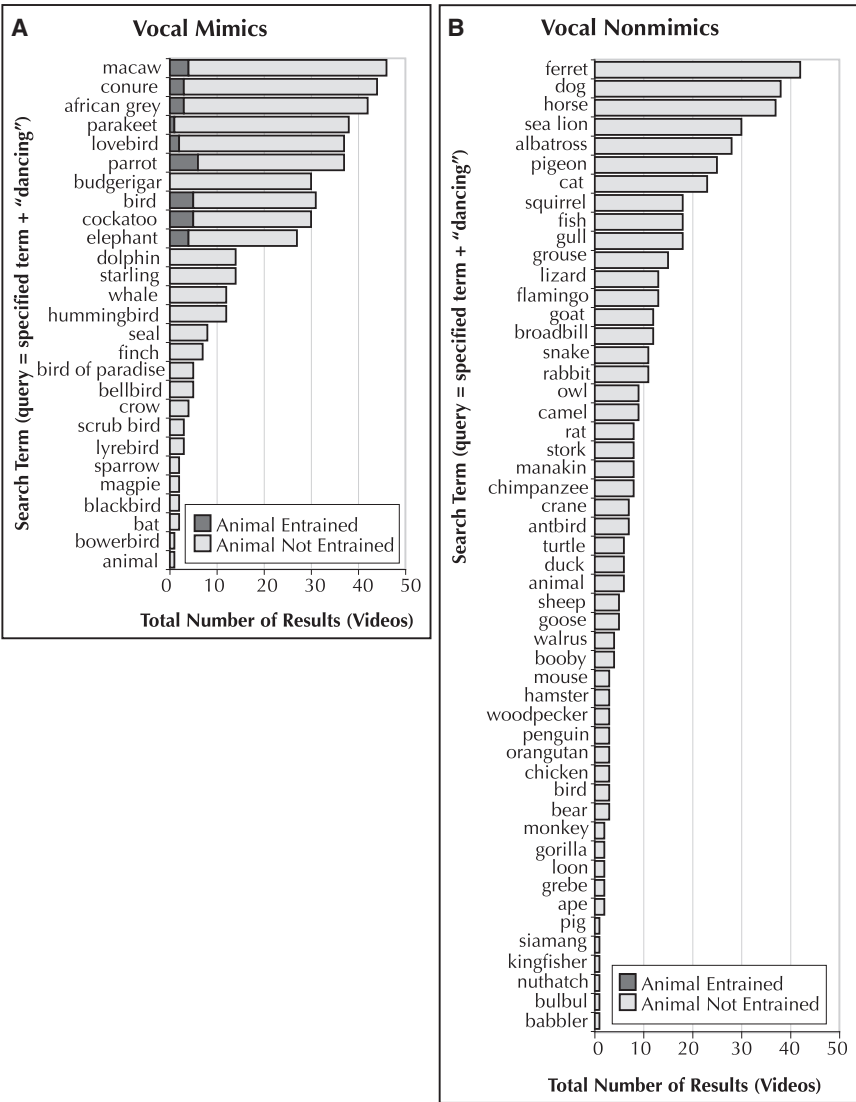


Figure 2. Distribution of Evidence of Entrainment across Species

Distribution of animals showing evidence of entrainment in vocal mimicking (A) and vocal nonmimicking (B) species in an online database. (See Supplemental Experimental Procedures for definition of vocal mimicry.)

data led to the hypothesis that selection for vocal mimicry resulted in modifications to the basal ganglia, creating the tight auditory-motor coupling that also forms the foundation for entrainment [12, 13].

Our results support this hypothesis. First, detailed case studies demonstrated the capacity for entrainment in two vocal mimicking animals. In addition, we found that evidence of entrainment exists in a variety of vocal mimicking species (humans, numerous parrot species, and elephants) while remaining conspicuously absent in a large, diverse sample of vocal nonmimicking species. These two data sets provide significant support for the claim that vocal mimicry is a necessary precondition of entrainment.

To our knowledge, avian species do not entrain to auditory beats in their natural behavioral repertoire. If an observed behavior does not exist in the natural behavioral repertoire, it has no potential to increase or decrease fitness and thus cannot be directly selected for or against. Because vocal mimicry seems necessary for entrainment but entrainment does not appear in the natural behavioral repertoire of birds, the avian capacity for entrainment most

likely evolved as a by-product of selection for vocal mimicry, and not vice versa.

Why humans produce and enjoy music is an evolutionary puzzle. Although many theories have been proposed [28–33], little empirical evidence speaks to the issue. In particular, debate continues over the idea that the human music capacity was not selected for directly but arose as a by-product of other cognitive mechanisms [5, 13, 33]. By supporting the idea that entrainment emerged as a by-product of vocal mimicry in avian species, the current findings lend plausibility to the idea that the human entrainment capacity evolved as a by-product of our capacity for vocal mimicry.

Discussion

Supplemental Data

The Supplemental Data include Supplemental Experimental Procedures, Supplemental Results, Supplemental Discussion, three tables, two figures, and two movies and can be found with this article online at [http://www.cell.com/current-biology/supplemental/S0960-9822\(09\)00915-4](http://www.cell.com/current-biology/supplemental/S0960-9822(09)00915-4).

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It has recently been hypothesized that the capacity for entrainment evolved as a by-product of selection for vocal mimicry [12, 13]. Like vocal mimicry, entrainment involves a specialized, modality-specific link between auditory and motor representations: stimuli in other modalities, such as visual rhythms, do not support accurate entrainment [1, 25]. In addition, the evolution of vocal mimicry in avian species is associated with parallel modifications to the basal ganglia, the same mechanisms that support musical beat perception in humans [26, 27]. These

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